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GALLS INDUCED ON HOPEA PONGA (DIPTEROCARPACEAE)
IN SOUTHERN INDIA AND THE GALL-MAKER BELONGING
TO THE BEESONIIDAE (HOMOPTERA : COCCOIDEA)

By ANANTANARAYANAN RAMAN and SADAO TAKAGI

Abstract

RAMAN, A. and TAKAGI, S. 1992.   Galls induced on *Hopea ponga* (Dipterocarpaceae) in southern India and the gall-maker belonging to the Beesoniidae (Homoptera : Coccoidea).   *Ins. matsum. n. s.* 47: 1-32, 36 figs.

Spherical echinate galls are induced on *Hopea ponga* by *Mangalorea hopeae* Takagi, gen. et sp. nov., in southern India.   Galls arise in leaf axils through modification of the vegetative bud which develops into a massive columella: differentiation and development of leaf primordia are completely arrested, but the surface initials of the columella develop into multicellular echinate appendages.   Each mature gall contains only one female, whereas a number of male insects occur on their maternal gall, occupying spaces between echinate appendages.   *M. hopeae* is unusual in lacking caudal setae in the 1st instar, which is unique among the known beesoniids also in having acorn-shaped setae ; the adult female is not enclosed by the skin of the preceding larval instar and is characterized by having 'warts' or much modified setae ; the adult male is peculiar in having numerous papillae over the body.

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Contents

Part I

GALLS INDUCED BY MANGALOREA HOPEAE ON HOPEA PONGA (DIPTEROCARPACEAE) IN SOUTHERN INDIA

By A. RAMAN

INTRODUCTION

Indo-Malayan subregion includes a variety of coccoid galls that occur predominantly on species of Casuarinaceae, Dipterocarpaceae, Fabaceae, Fagaceae, Malvaceae, and Myrtaceae (Maskell 1891, Green 1896, 1900, Houard 1922, Docters van Leeuwen 1925*, Docters van Leeuwen-Reijnvaan and Docters van Leeuwen 1926*, Beeson 1941, Mani 1973, Anthony 1974). Among these, the family Dipterocarpaceae, a highly diverse group with c. 250 arborescent species, is associated with coccoids bearing exquisite stem and leaf galls. For example, *Gallacoccus* (Eriococcidae) induces epiphyllous bud galls on *Shorea* (Anthony 1974); *Beesonia* (Beesoniidae) induces durian-fruit like galls on *Dipterocarpus* (Green 1928, Beeson 1941, Corner 1963). In this paper I describe the gall induced by a beesoniid, *Mangalorea hopeae*, on *Hopea ponga* (Dennstedt) Mabberley (=*H. wightiana* Wall.) in southern India. Previously I (Raman 1988) described this gall as being induced by a *Beesonia* species, but at that time I confused instars of the coccoid; therefore, that description should be replaced by this paper.

MATERIAL AND METHODS

Galls in different developmental stages were collected from the west coast of peninsular India (for details, see Part II of this paper). They were fixed in FAA (Formalin : Acetic acid : Alcohol [70%] = 5 : 5 : 90) for 36 h and processed through customary methods of dehydration and wax embedding. They were cut at 6-8 μm and stained with 1% toluidine blue [in 1% aqueous borax]. Specific histochemical procedures followed are indicated at pertinent points.

THE NATURAL HISTORY

Galls of *Hopea ponga*, shaped like a sea urchin, occur generally in leaf axils and rarely on shoot terminals. Mature galls are dark green and spherical (3.0 cm in dia.) with numerous thick and pointed structures. With maturation, these galls change colour from pale to dark green, then to brownish green, and finally to grey, losing simultaneously their spherical shape by developing irregular cracks. Usually only one gall occurs in an axil, though occasionally more than 3 crowd in one (Fig. I.1). In such multiple gall situations, the gall occurring away is larger than the one at the axil, suggesting the former to be the oldest of the group.

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* These authors report galls on *Dipterocarpus tuberculatus* and *Hopea fagifolia* from Siam and Netherland East Indies, supposedly made by an undetermined insect and a midge, respectively. From the illustrations, I suspect them to be beesoniid galls.

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A mature gall has a stalk (0.2-0.4 cm) that expands rather abruptly into a spherical part, from which a number of hard, elongated structures project. For descriptive reasons, the spherical part will be referred to as columella and the sharp, elongated structures as echinate appendages. At the angle created by the attachment of the gall stalk to *Hopea* stem, an adult female coccoid occurs like an inflated saccular object covered by the lower parts of the spherical columella. The adult female fits snugly in the available space, and hence is well protected by the peculiar gall shape. In every gap available between two adjacent appendages one male nymph occurs, with its head end pointing towards the spherical columella, and grows into the adult (Fig. I.2). Mature galls in median vertical sections show a fine curve in columella's shape; because of curvature, the shape and texture of appendages that occur on it vary subtly, though with no remarkable internal or external variation. Especially in regions of curvature, distribution of appendages is sparser and they are thinner than those occurring on the other side of the same gall.

Vegetative shoot buds of *Hopea ponga* are densely tomentose and extraaxillary, occurring at *c*. 2.0 mm above the axillary angle. Internally, they show normal structures of a shoot meristem, recognizable as tunica and corpus layers, and covered by an epidermis with several unicellular hairs (Fig. I.3).

Soon after the monsoon rains, freshly emerged instar I female nymphs of *Mangalorea hopeae* invade the axillary angles of vegetative buds, exploiting the space created by their extraaxillary positions. Once settled, the nymph begins to feed on the undifferentiated cortical tissues of the bud. The feeding stimulus restricts the bud from developing into an axillary branch; instead, it develops into a gall (Figs. I.4 & .5), resulting in an eccentrically grown massive columella that arches over the inhabiting coccoid (Fig. I.6). The female derives its nutrition from the cortical parenchyma cells of bud modified to grow into the gall. These cells show active cytoplasm and prominent nuclei with signs of metaplasia (Fig. I.7). Vascular traces ramify through the columella and due to its intense expansive growth, lysigenous cavities develop (Fig. I.8). Subsequent growth of the columella takes place essentially due to hyperplasia of the central medullary cells (Fig. I.9). Simultaneously with the arching growth of the bud meristem, some of the epidermal and subepidermal cells become active and differentiate into multicellular, vascularized echinate appendages (Fig. I.10 & .11). Modification of these cells into hard appendages occurs sufficiently early during gall growth. Obviously, the stimulus provided by the feeding activity of the growing female nymph that occupies the axillary gap of *Hopea* activates the epidermal and subepidermal cells to become multicellular appendages (Fig. I.12). Initially, these appendages differentiate their lancelike terminal part (Fig. I.13). When mature, each of these appendages has a slim stalk bearing the lanceolate part (Fig. I.2) with several unicellular emergences. These echinate appendages show considerable variations in size (length: 2.5-12.0 mm; width of the basal stalk: 0.3-1.8 mm; width of the upper lancelike part: 0.5-3.5 mm). The unicellular emergences of appendages on mature galls have highly lignified walls with polyphenolic inclusions (Lugol's Iodine test–Johansen 1940) (Fig. I.14).

In old galls, tissue behaviour of the columella is more striking than that of the appendages. With ageing, parenchyma cells of the columella become lignified. Signs of subcellular degeneration become evident: cells show hyaline, peripheral

cytoplasm and intense accumulation of polyphenolic materials. Rupture of vascular strands disrupts water and nutrient supply to the gall. Lignified parenchyma cells separate from one another due to dissolution of middle lamella and develop large cavities. Cells bordering the gall stretch horizontally, thus pulling laterally the appendages that occur on them. This lateral movement of appendages facilitates the escape of adult males from the gall.
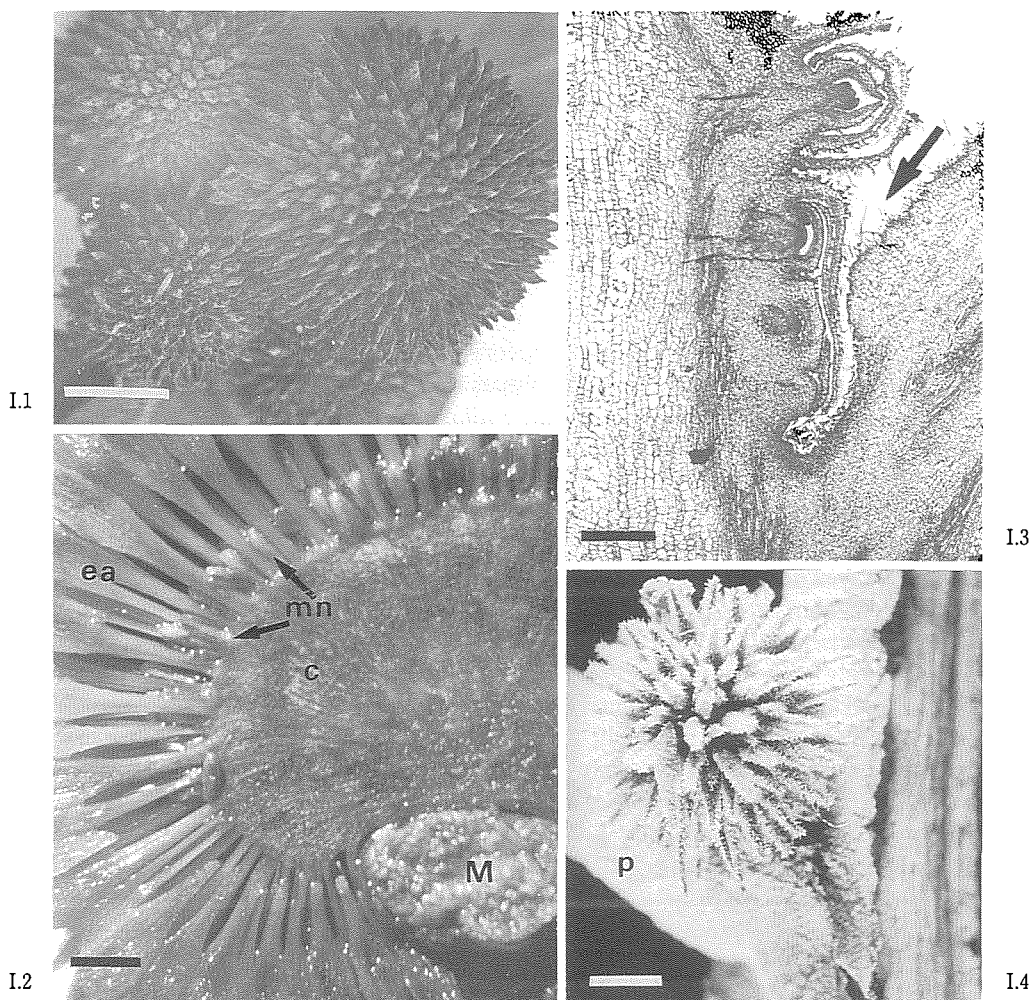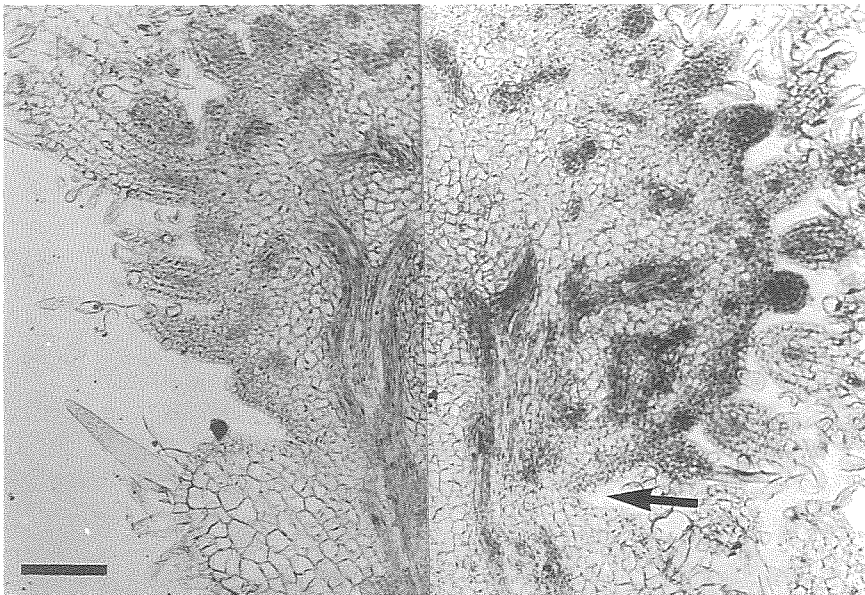

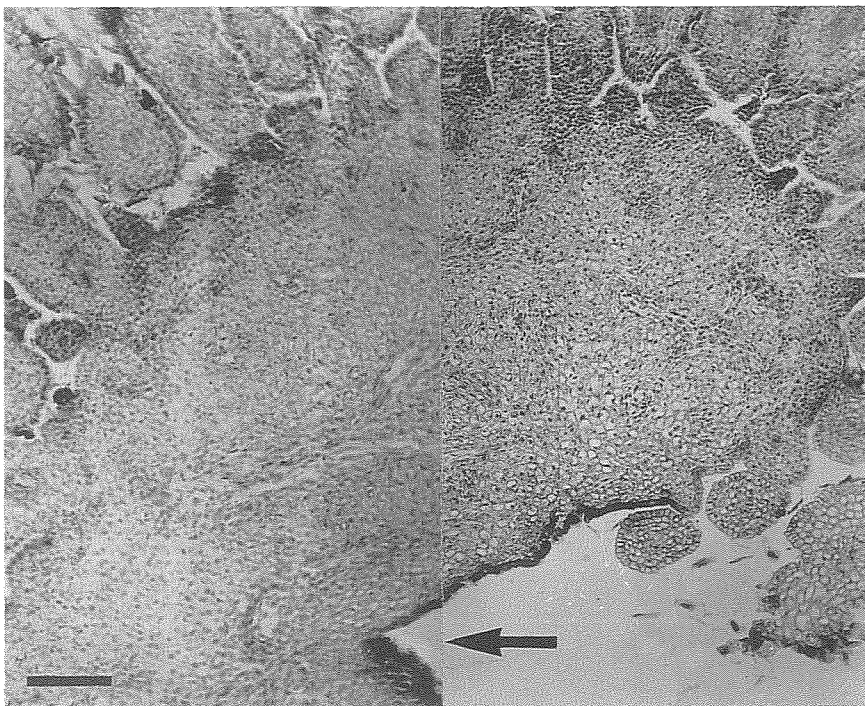Fig. I.1. Gall cluster of *Hopea ponga*. Bar = 1.0 cm.
Fig. I.2. Mature gall (V.S.). c-columella; ea-echinate appendages; M-*Mangalorea* female; mn-male nymphs. Bar = 2.0 mm.
Fig. I.3. Normal vegetative bud of *Hopea ponga* (V.S.). Arrow-axillary angle. Bar = 200 μm.
Fig. I.4. Young gall with soft echinate appendages and an insignificant columella. p-petiole of the subtending host leaf. Bar = 2.0 mm.

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Fig. I.5. Young gall (V.S.). Intense parenchymatization of the shoot bud with differentiating appendages. Arrow-position of the invading *Mangalorea* female nymph. Bar=100 μm.

Fig. I.6. Young gall (V.S.). Eccentric growth of the columella. Arrow-nymphal position. Bar=100 μm.
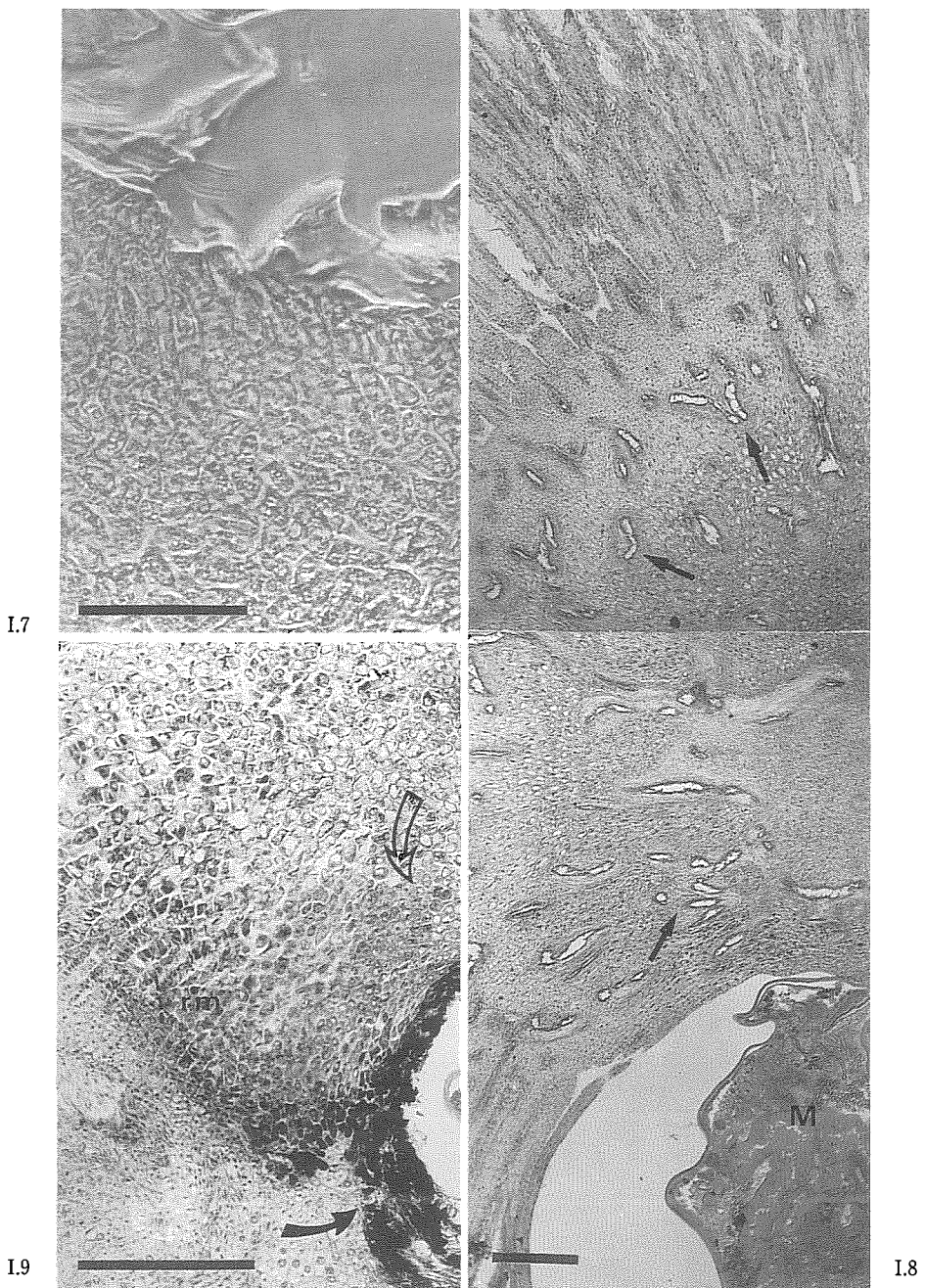
Fig. I.7. Young gall (V.S.). Nutritive tissue of the female nymph. Cells show intense cytoplasm
and stages of metaplasia (phase contrast microscopy). Bar=50 μm.

Fig. I.8. Mature gall (V.S.). M-*Mangalorea* female. Arrows-columellar lysigenous cavities.
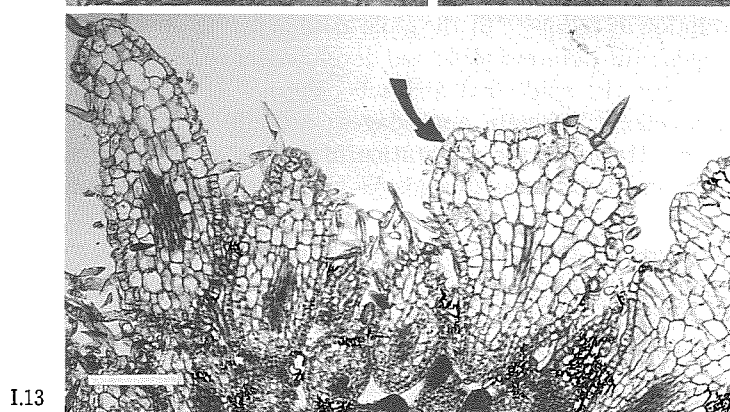Bar=100 μm.

Fig. I.9. Mature gall (V.S.). Nutritive tissue of *Mangalorea* female. Open arrow-region of
current feeding; closed arrow-necrosed region where the insect fed earlier; rm-active
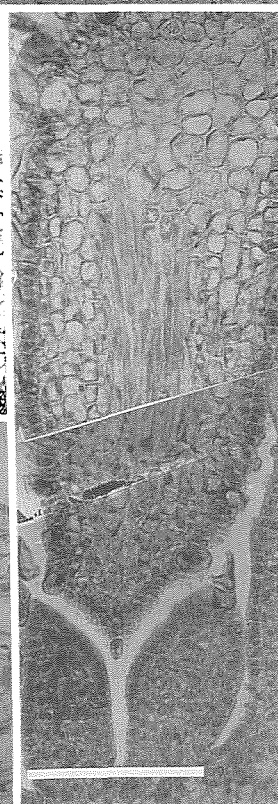differentiation of rib meristem contributing to the bulk of the gall. Bar=100 μm.

I.10

I.11

I.13

I.12

I.14
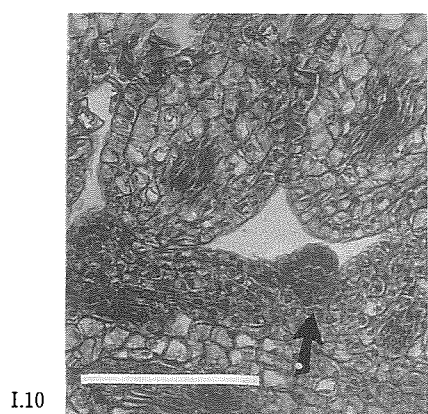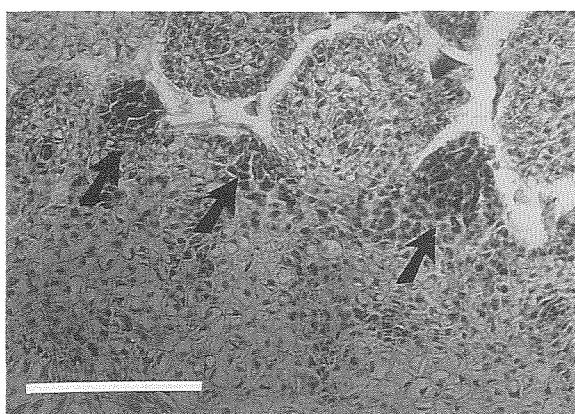
Figs. I.10, .11 & .12. Young galls (V.S.). Stages of development of echinate appendages from columellar surface. Bar=100 μm.

Fig. I.13. Young gall (V.S.). Developing echinate appendages showing the earlier differentiation of the lanceolate part. Bar=100 μm.

Fig. I.14. Mature gall (V.S.). A mature echinate appendage with unicellular emergences. Open arrow-a tender emergence showing a nucleus; closed arrows-emergences with lignified walls and polyphenolic inclusions. Bar=50 μm.

1. Green (1928) describes galls of *Beesonia dipterocarpi* on *Dipterocarpus tuberculatus* as follows: "...the large foliaceous galls...appear to develop at the extremities of the smaller branches of the tree and to result from an conglomeration of hypertrophied leaf-buds. ...., the insects occupy separate cavities in the woody core. A medium-sized gall may contain as many as a dozen fully developed females. Each insect rests with its posterior extremity directed outwards, usually in close connection with a crevice leading to the surface. The opposite extremity appears to be attached to the lining tissue of the cavity. Very old individuals may have the whole surface rigid and densely chitinised, but the anterior half of the body is usually colourless and membranous. In the crevices of the galls are crowded great numbers of the earlier stages of the male insects". Galls of *Mangalorea hopeae* on *Hopea ponga* differ from this description as follows: (i) the galls arise in leaf axils through modification of vegetative buds; (ii) differentiation and development of leaf primordia are completely arrested, but the epidermal and subepidermal initials of the columella develop into multicellular echinate appendages; and (iii) each mature gall contains only one female. However, the orientation of the female within the gall and distribution of male nymphs between appendages indeed make *Mangalorea* and *Beesonia* galls comparable.

2. Two principal life stages of *Mangalorea hopeae* participate in *Hopea* gall system: (i) an individual instar I female nymph initiates the gall on a vegetative shoot bud exploiting the axillary gap; (ii) a number of male nymphs, supposedly emerging from that female after its maturation and mating, occupy spaces between echinate appendages. The males occurring between appendages contribute to the alteration of gall physiology by their feeding activity, particularly in an ageing gall. By their number, they tend to utilize more vigorously the nutrient resources than what an ageing gall can mobilize; this process probably accelerates drying of gall.

3. Occupation of the maternal gall by a number of males is not unique to *Mangalorea*. A cecidogenous eriococcid, *Cystococcus*, too, shows this behaviour that the male offspring complete their development within the maternal gall on *Eucalyptus*, feeding on a layer of nutritive tissue lining the gall cavity (Gullan and Cockburn 1986).

4. Terminal regions of generative buds are not damaged during gall induction, since the gall-initiating female *Mangalorea* feeds only along the sides. The cecidogenetic gradient triggered by the feeding stimulus spreads to apical parts of the gall, promoting a sudden expansive growth of the host bud developing into the gall columella. With the disturbance of normal morphogenetic controls, the transformed apex, in stead of developing leaf primordia (and later into a branch), undergoes intense parenchymatisation and negotiates a curvature, providing cover to the gall-initiating female simultaneously. Cecidogenetic stimulus also triggers an unusual developmental course transforming columella's surface cells into multicellular, vascularized appendages. During their initial phase of growth, the terminal, lancelike parts exhibit a more active growth than the lower stalk regions of these appendages. Lancelike parts of adjacent appendages occur so closely that they afford physical protection to the inhabiting nymphs. Lignified emergences occurring on the lancelike part include polyphenolic materials which should necessarily

offer physiological protection to nymphs from any invading predator. Lower stalk region of each appendage elongates more by stretching than by cell division and the entire appendage complex is strengthened by the vascular network of the columella. With maturation, columellar cells stretch in horizontal axis due to desiccation resulting in the separation of appendages, thereby facilitating the escape of adult males.

5. Broadly speaking, the cecidogenetic pattern of *Mangalorea hopeae* can be compared with that of *Gallacoccus anthonyae* (Eriococcidae) reported by Anthony (1980a). Both the galls of *Mangalorea* and *Gallacoccus* are pathological buds, although the gall of the latter is essentially epiphyllous. In both, the I instar nymphs initiate galls. Through the action of *Gallacoccus,* the epiphyllous buds of *Shorea* differentiate scale leaves in a distichous manner and show 2 clear organogenetic periods interspersed by a rest period ; but in *Mangalorea* galls, the bud differentiates neither normal nor scale leaves, but becomes a massive column of parenchyma and offers nutrition to the growing female nymph. Progeny of the gall-inducing *Gallacoccus* female invade the undersides of newly formed scale leaves of the gall, while that of *Mangalorea* invade spaces between newly formed echinate appendages.

6. Epidermal and subepidermal cells of normal shoot bud get transformed into large, multicellular echinate appendages. Alteration in the growth mechanics of these appendages synchronizes with the discharge of male nymphs from the gall-initiating female occurring below. Besides offering protection from predatory organisms, spaces between appendages offer nutrition to male nymphs. This emphasizes the adaptive response nature of the host to the biological stages of the coccoid.

7. Gall-inhabiting *Mangalorea* female feeds on the cortical parenchyma cells of the vegetative bud, while the male nymphs preferentially feed on gall columella's phloem strands. Ability to acquire nutrition from parenchyma cells besides phloem at least during one phase of development appears striking. This trait is shared by *Gallacoccus* (Anthony 1977).

8. The available details show that an adult male mates with the female that lies trapped within the gall. Developmental process of the gall is such that it does not cover the female entirely. A small aperture exists closer to the stalk and the adult female within the gall has its anal-genital region positioned at that point. This orientation of the female probably enables (i) the male to mate with the gall female from outside and (ii) the nymphs, probably developing viviparously, to be discharged. A similar behaviour of males mating with females entrapped within galls of *Casuarina* occurs in the eriococcid *Cylindrococcus spiniferus* (Gullan 1978).

9. Patterns of cecidogenous interaction between dipterocarps and coccoids (eriococcids and beesoniids in particular) appear fascinating. Anthony (1980b) has indicated an apparently 'specific' relationship of *Gallacoccus* with several Malay dipterocarps. This work on an Indian speices, *Mangalorea hopeae,* too, supports this rather queer tie-up, which, of course, needs to be rationalized after deeper biochemical evaluations.

ment, and critical reading of the manuscript. I appreciate the interest of Professor Sadao Takagi in clarifying a few critical problems relating to the biology of the coccoid. This work was done with a research grant (SP/SO/C-35/88) from the Department of Science & Technology (Government of India, New Delhi).

Part II

MANGALOREA HOPEAE, A NEW BEESONIID (HOMOPTERA: COCCOIDEA) INDUCING GALLS ON HOPEA PONGA IN SOUTHERN INDIA

By S. TAKAGI

INTRODUCTION

The family Beesoniidae, erected by Ferris (1950) for 2 species known at that time, is a group of odd coccoids. I (Takagi, 1987) recognized 3 distinct species in the family, and referred them all to *Beesonia* tentatively. The species described in the present paper represents another genus of the family. These species are enumerated below for convenience of reference and discussion.

Beesonia dipterocarpi Green, 1926. Burma, on *Dipterocarpus* [Dipterocarpaceae]. Inducing 'large foliaceous galls...at the extremities of the smaller branches of the tree' (Green, 1928).

Beesonia napiformis (Kuwana, 1914) [originally *Xylococcus napiformis*] (= *B. quercicola* Ferris, 1950; = *B. albohirta* Hu and Li, 1986). Japan, Korea, China and Nepal, on *Quercus, Lithocarpus* and *Castanopsis* [all belonging to the family Fagaceae]. The female only is known. Occurring on twigs and branches. Usually many individuals are found together, causing swellings of affected twigs and branches and inhabiting pits formed in response to their feeding. The bark of the affected parts are roughened and cracked apparently owing to the swelling. These deformations of the host plant may deserve to be called a stem gall.

Beesonia brevipes Takagi, 1987. Nepal, on *Quercus*. Females living in pits formed on twigs and branches. (Another form very close to [conspecific? with] this species occurs in Japan on *Castanopsis*.)

Mangalorea hopeae, described in this paper.

B. *napiformis* and B. *brevipes* are remarkably different from B. *dipterocarpi* in host association and gall-making habit. However, they are tentatively referred to *Beesonia* Green, 1926, partly because our knowledge as to B. *dipterocarpi*, the name-bearing species of the genus, is still incomplete and confused.

DESCRIPTION

Mangalorea hopeae Takagi, sp. n.

Material. From *Hopea ponga* (Dennstedt) Mabberley (= *H. wightiana* Wall.) [Dipterocarpaceae] in southern India: Udupi Region, near Mangalore Coast, Feb. 1990, and Wynaad Region, Kozhikode [Calicut], May 1990, coll. A. Raman.

The female induces galls on vegetative axillary buds. The gall is a spherical mass, about 2.5 cm across at maximum, borne on a short stalk and covered by spinous processes, thus appearing like a sea urchin (Fig. II.1); always 1 female of M.

hopeae occurs in a gall, with a small part of the body (probably the anal-genital area) exposed through a small hole on the gall beside the stalk.

Males occur on the exterior surface of the gall among spinous processes, which are lanceolate, with the stalk elongate and slender, thus forming a space to accommodate the insect body between. They hold the body along the stalks, with the head directed to the main body of gall (called 'columella' in Part I). Pupae and adult males were found within white secretion.

First instar males and females, intermediate instar males (probably belonging to the last larval instar), pupae, and adult males and females were mounted. However, the mounted specimens of the adult female were not in good condition. A few adult females were observed in a scanning electron microscope, but the observations were far from complete and satisfactory owing to their condition. Adult males were prepared after the same method as with other stages and mounted with fragments of cover-glass (0.12-0.17 mm thick) aside. One specimen of an intermediate instar female was also examined.

Name-bearing specimen [holotype] : 1st instar female from the Udupi Region ; deposited, together with some other specimens, in the collection of the Zoological Survey of India, Calcutta.

First instar female (Figs. II.2, .3 & .17). Body of newly hatched female ovoid, with the posterior end (supposed 8th abdominal segment) truncate. Dorsal surface of abdomen with a distinct segmentation ; segments I-VI each with a transverse sclerotized area, which is irregularly interrupted by longitudinal membranous lines ; VII and VIII fused marginally and sclerotized ; IV and V each with 3 pairs of triangular processes along the posterior margin, the lateralmost pair often reduced in size or obsolete. Ventral surface of abdomen poorly segmented ; segments I-VII each with a sclerotized area laterally ; VIII sclerotized, enclosing a round well-sclerotized plate bearing anus ['anal plate'].

Antennae 3-segmented, segments I and II short, III elongate, longer than the basal 2 segments combined (antenna 44-52 and segment III 28-32 μm long ; n=10) ; segment II narrowly sclerotized basally, with a slender seta and a round sclerotized tubercle near apical margin ; segment III with 7 long setae toward the apex, 3 of them being thickened.

Tibia elongate, with a seta ventrally near apex ; tarsus as long as tibia in fore and mid legs, as long as or a little longer than tibia in hind leg (in hind leg, femur and trochanter combined 68-78, tibia 38-44, tarsus 44-49, and claw 14-16 μm long ; tarsus/tibia 1.0-1.2 ; n=10), with 2 setae ventrally and a short seta dorsally in addition to 2 long capitate setae ; claw with a minute tooth on plantar surface.

Setae on cephalothorax mostly acorn-shaped (short and thick, round basally, with a short, blunt projection apically), the basal socket being situated on a slight swelling of derm ; these modified setae being scattered over dorsal surface, but limited to submarginal region and tending to be arranged in short oblique rows on ventral surface, most if not all pointing backward ; head with long, slender setae medially : 1 pair dorsally near anterior margin and 3 pairs ventrally between anterior margin and mouth-parts. Abdomen dorsally with a pair of setae medially on segment I and 2 pairs submarginally on the united segments VII and VIII, all these setae being slender, short and stiff. Ventral surface of abdomen with a double row of submarginal setae through the segments, the anterior 4 setae in the outer series

being acorn-shaped. Anal plate with a pair of small setae. Caudal setae absent (no usual long caudal setae are found).

Ducts slender, with the inner end divided by a median partition, thus presenting a figure 8 appearance when viewed from above [geminate-pore type ducts], mostly scattered over dorsal surface of cephalothorax ; abdominal segments III, V and VII each with a pair of ducts submedially on dorsal surface ; there are a few ducts also on ventral surface. Spiracles each with a 5-locular disc pore.

Anus small, semicircular or crescent-shaped, situated about centre of anal plate, bearing a spatulate projection on posterior margin ; it seems that normally this projection covers the anal opening [so that it may be called 'anal operculum'].

First instar male (Fig. II.18). Differs from the 1st instar female as follows. Body with posterior end not truncate but round ; derm membranous ; anal plate situated dorsally, with 2 pairs of setae, these and other setae occurring around the anal plate are stiff and apically blunt ; anal operculum on anterior margin of anal opening. Only some setae occurring on the thorax and the base of the abdomen within the margin are modified into acorn-shaped ones, which are much smaller than in the female. Ducts fewer. There is a longitudinal row of submedian setae dorsally through the meso- and metathorax and abdomen. Submarginal setae forming a single longitudinal row ventrally through abdomen ; there are setae on the margin of the abdomen, instead. Derm of abdomen with spinules and crenulae on both surfaces. There is a round, somewhat sclerotized patch laterally to the hind coxa ; this patch has a centre, from which some creases radiate, but the true nature of this structure is unknown. Legs shorter and robust (in hind leg, femur and trochanter combined 64–70, tibia 29–33, tarsus 34–37, and claw 14–16 μm long ; n= 10). Antennal segment III with 2 infrasegmental constrictions (thus appearing as if 3-segmented) (antenna 47–56 and segment III 27–32 μm long ; n=10).

Intermediate instar male (Figs. II.4–. 6 & .19). (Collected from the surface of galls together with pupae and adult males, probably belonging, therefore, to the last larval instar.) Body elongate (about 2.2–3 times as long as wide in the slide-mounted specimens), with the lateral margins nearly parallel and both ends rounded ; membranous, strewn with numerous ducts and processes (spinules, crenulae and tubercules) on both surfaces. The ducts are truncate on the inner end, from the rim of which arises a delicate filamentous prolongation ; the opening of the duct is round and surrounded by a slender rim. Much smaller ducts, of the geminate-pore type, also occur, but are very few and confined to the marginal region. Quinquelocular disc pores occurring on abdominal segments V–VII on both surfaces in lateral region, variable in number, but usually numerous. Spiracles usually with a 5-locular disc pore. Setae on head flagellate ; those on posterior end of body stiff.

Antennae situated between anterior margin of head and mouth-parts, separated from each other by width of mouth-parts ; each antenna is a low, sclerotized tubercle, with some setae unequal in length and thickness. Legs represented by strongly sclerotized conical processes ; 3 or 4 divisions or segments are evident, the basal-most segment is a slender ring and the apicalmost is shaped like a claw. Anal plate situated on ventral surface, with 2 pairs of stiff setae ; anal operculum on anterior margin of anus.

Adult female (Figs. II.7–. 14, .20 & .21). Body globular (about 8.5 mm in length and 6 mm in width in a slide-mounted full-grown individual). Derm membranous

throughout. Antennae and legs absent.

Mouth-parts with a pair of remarkable appendages, which are well stained, fanlike in shape, and thickly striped transversely (Fig. II.7) ; another interior structure, a belt in an arch similarly striped, is laid across within the posterior half of the body (Fig. II.8) ; there are some patches, also striped, arranged in a circle around anal-genital area (Figs. II.9 & .10). The true nature of all these structures is unknown, but they may be secondary outgrowths, because they are ill developed or absent in immature adult females ; while the patches are ventral, the belt seems to grow from the dorsal derm.

Derm beset with small processes of an unusual type, which may tentatively be called 'warts' (these are almost absent in the region encircled by the spiracles and in the caudal region of the body). The wart, when observed by scanning electron microscopy, is composed of 3 parts, body, head and collar, and is laid sideways : the body is a swelling ; the head is a flatly round prominence and separated from the body by a double fold, lying on the collar, which appears to be an extension from the body (Fig. II.13). In light microscopy the collar is sclerotized and well stained (Fig. II.20). Most if not all warts pointing backward. Minute ducts of the geminate-pore type are scattered among warts. Setae stiff, abundant on posterior end of body.

Anterior and posterior spiracles same in size, situated in a broad central region of ventral surface, each spiracle laterally with many 5-locular disc pores and warts crowded together (Figs. II.11 & .12).

Anal plate situated on ventral surface near posterior end of body ; anus small, crescent-shaped, with anal operculum on anterior margin. Stiff setae are strewn in front of the anal plate, and anterior to this region lies a transverse slit, which is interpreted as the genital opening. The supposed genital slit is combined with a transverse area just anteriorly ; this area is strongly sclerotized on the lateral sides, where it seems to be slightly swollen ; stiff setae occur in the middle region of the area, and minute setae (the setae themselves are much reduced in size, but their basal sockets are as large as those of the middle setae) are strewn inside the sclerotized lateral sides (Fig. II.21).

Adult male (Figs. II.15, .16 & .22). Macropterous form only known. Body slender, the abdomen about 1.5 times as long as head and thorax combined, tapering toward apex. Head, antennae, thorax, legs and abdomen beset with numerous small, elongate processes or papillae ; setae mostly intermingled with papillae.

Head in dorsoventral view rounded, constricted just anteriorly to tubercular ocelli. Arms of midcranial ridge joined together, the dorsal arm short. Postoccipital ridge laterally giving off 2 branches, one anteriorly and the other posteriorly. Preocular ridge short, connected with postocular ridge through interocular ridge. Corneae of dorsal and ventral simple eyes subequal in diameter.

Antennae 3-segmented, subequal in length (404-448 μm ; n=10) to hind femur, tibia and tarsus combined. Basal segment short, subquadrate, with 2 setae on anterior margin, without papillae. Segment II rounded, with a few setae and some papillae on ventral surface. Segment III very long (332-372 μm ; n=10), more or less constricted 3 or 4 times, the apicalmost constriction always deep, making the apical section distinct ; with papillae except on base and apical section, and with long setae except on base, the apical section with especially long setae and with a pair of long, thick, falcate setae basally.

Scutum much shorter than prescutum. Scutellum transversely subrectangular, well sclerotized except for a crescent-shaped area medially. Postnotal apophysis well developed.

Wings with no circular sensoria. Halteres absent. Spiracles with no disc pores.

Legs stout, with tibia a little shorter than femur and with tarsus a little shorter than tibia (in hind leg, trochanter 92-104, femur 160-172, tibia 140-154, tarsus 112-124 and claw 32-40 μm ; n=10). Tibia and tarsus with many well-developed setae. Claw with a minute tooth on plantar surface.

Abdomen with segmental bands of papillae across, sternites III-VIII spiculate anteriorly to the bands. Genital segment forming a well-sclerotized capsule extending into style which is slightly curved in lateral view ; aedeagus straight in lateral view, a little exceeding style ; whole genital segment subequal to femur in length (Fig. II.16).

Mangalorea Takagi, gen. n.

Name-bearing species [type-species] : *Mangalorea hopeae.*

First instar female. *B. dipterocarpi, B. napiformis* and *B. brevipes* are commonly characterized in main features of the 1st instar female (this is another reason for the inclusion of all these species in the same genus) (Takagi, 1987). *M. hopeae* is similar to them in this stage especially in the structure of the antennae and in the sclerotized dorsal derm of the abdomen (the instar and sex were determined on the basis of this similarity). In some other features it is remarkably different from the *Beesonia* species, and the following characters may be adopted as generic :

    a. Many body setae are acorn-shaped.
    b. Anal plate roundish, with only 1 pair of small setae.
    c. Anal plate without side plates.
    d. Anal plate occurring on ventral surface.
    e. Anus with an operculum.
    f. Third antennal segment without a thick subbasal seta.
    g. Tibiae subequal to tarsi in length.
    h. Caudal setae absent.
    i. Ducts slender and much more numerous.
    j. Submedian dorsal setae absent on 2nd-8th abdominal segments.

First instar male. The male is unknown in *B. napiformis* and *B. brevipes.* In my examination of the 1st instar of *B. dipterocarpi* I supposed that 2 dintinct forms of larvae observed both belong to the 1st instar male (Takagi, 1987). Needless to say, this supposed dimorphism is quite unusual in Coccoidea and requires confirmation. The 1st instar male is, therefore, still problematical in *Beesonia,* and no comparison of this stage is here attempted between *Beesonia* and *Mangalorea.*

However, in *Mangalorea* most of the supposed generic characters of the 1st instar female are found in the 1st instar male. Characters d and j are not true for the 1st instar male. Characters a and b need to be modified : the acorn-shaped setae are much fewer than in the female and the anal plate is provided with 2 pairs of setae, which are small as in the female but are blunt apically.

Intermediate instars of female. The 2nd and 3rd instar larvae of *B. napiformis* and *B. brevipes* are known. Green's (1928) 'early and later nymphs' and 'adult
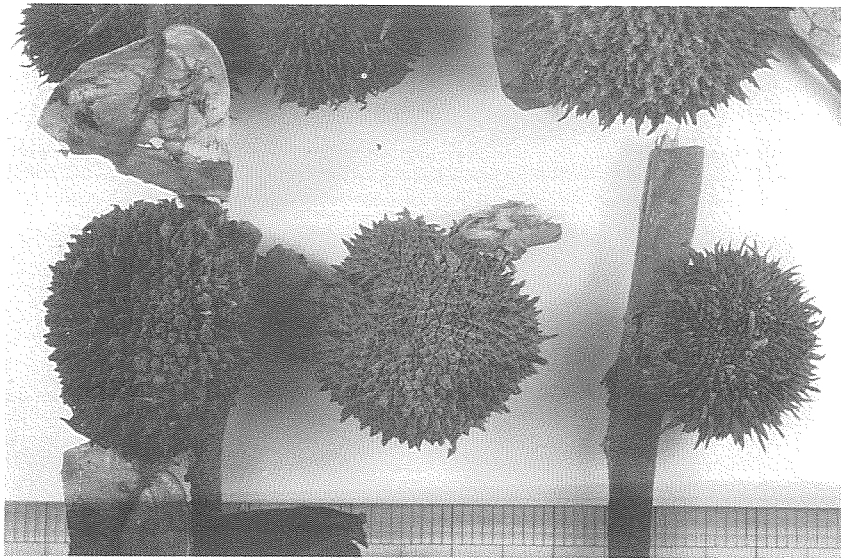
14

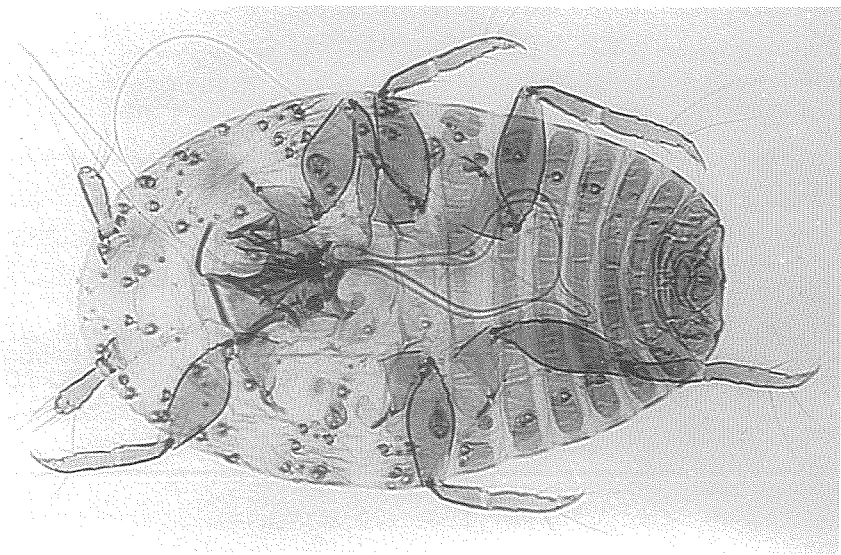Fig. II.1.　Galls formed on *Hopea ponga*.

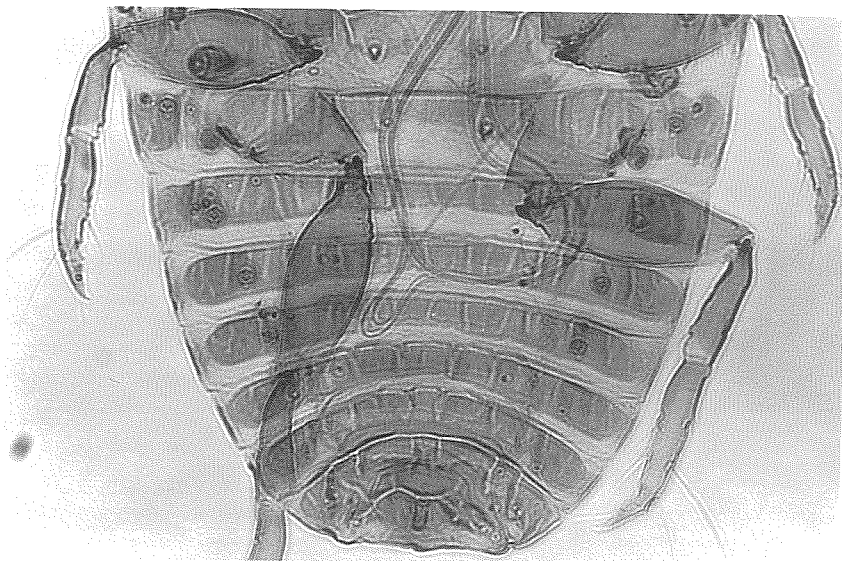Fig. II.2.　*Mangalorea hopeae*, 1st instar female.

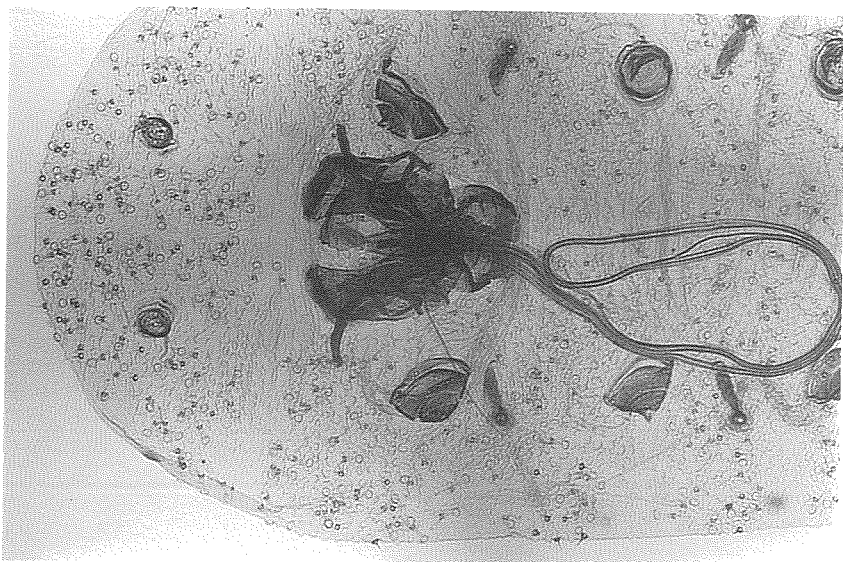Fig. II.3. *Mangalorea hopeae*, 1st instar female : abdomen.

Fig. II.4. *Mangalorea hopeae*, intermediate instar male : head and pro- and mesothorax.
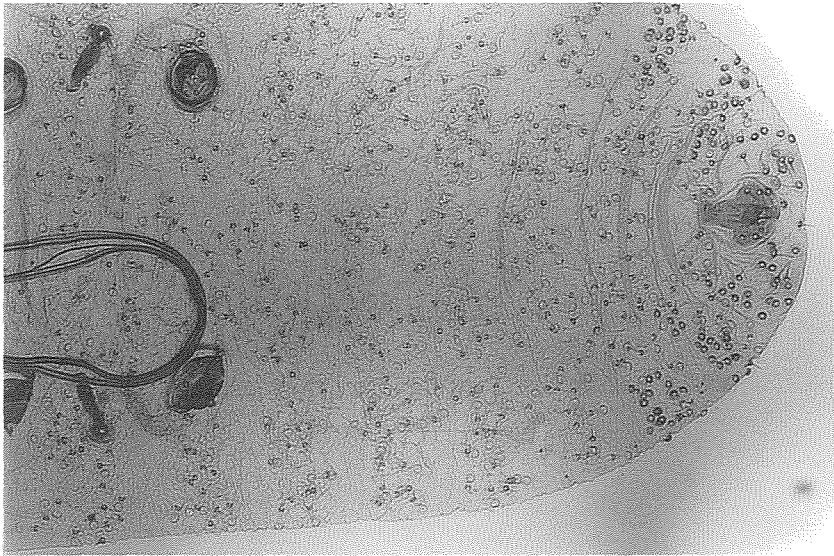
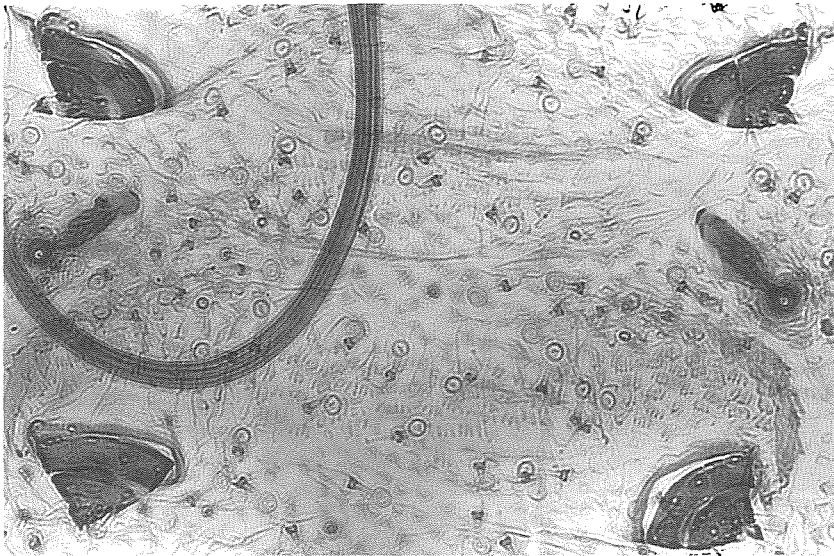Fig. II.5. *Mangalorea hopeae*, intermediate instar male : metathorax and abdomen.

Fig. II.6. *Mangalorea hopeae*, intermediate instar male : part of thorax, with mid and hind legs.
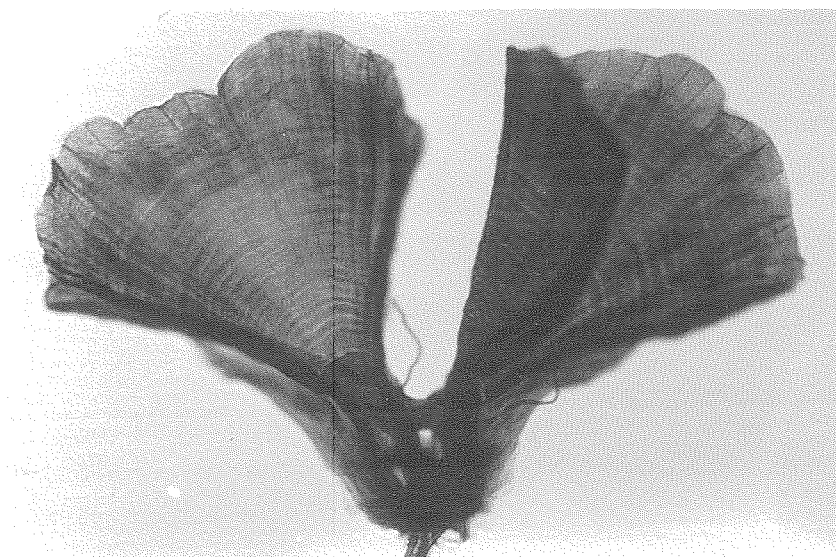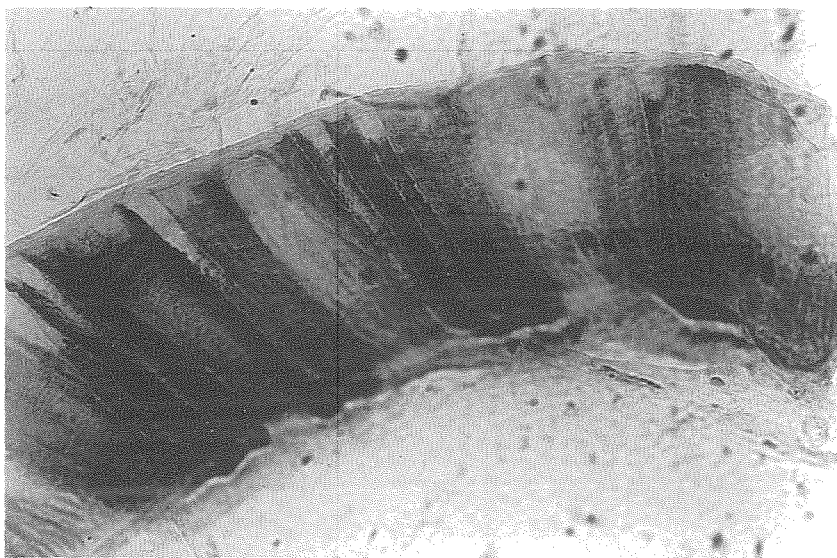
Fig. II.7. *Mangalorea hopeae*, adult female : mouth-parts.

Fig. II.8. *Mangalorea hopeae*, adult female : part of 'belt' within body.
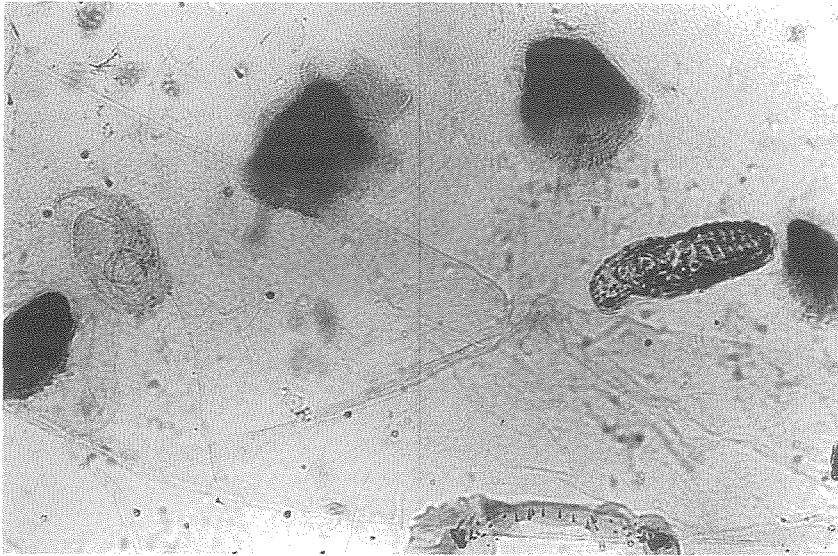
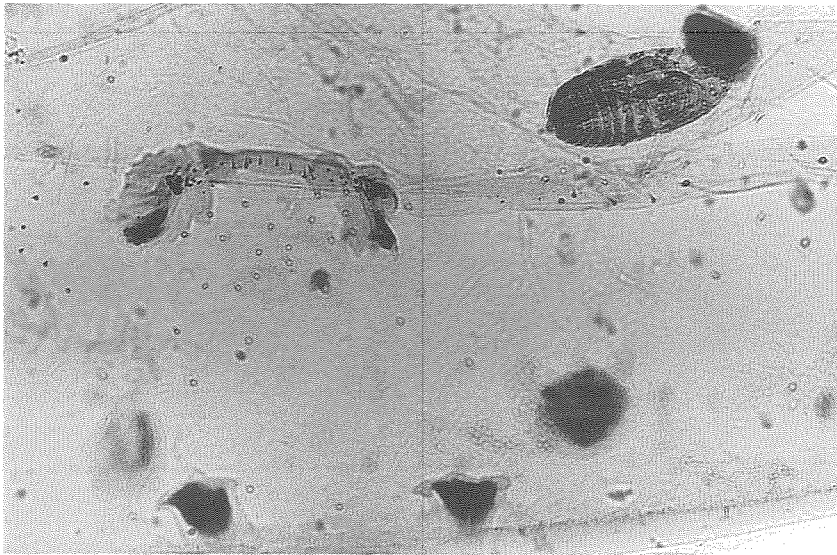Fig. II.9. *Mangalorea hopeae*, adult female: 'patches' around anal-genital area (genital slit in the bottom).

Fig. II.10. *Mangalorea hopeaé*, adult female: 'patches' around anal-genital area (this is toward the left anterior corner).
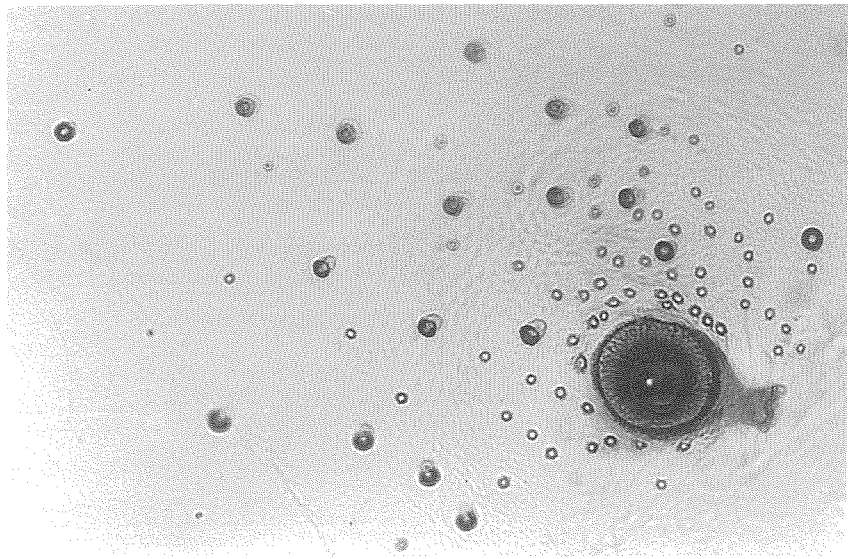
Fig. II.11. *Mangalorea hopeae*, adult female : spiracle, with warts and 5-locular disc pores.
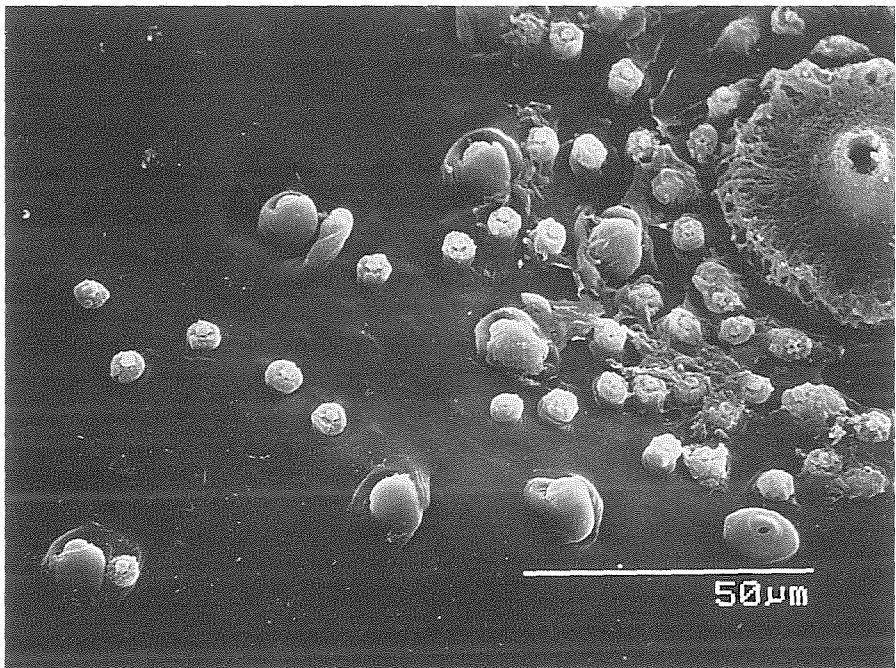

Fig. II.12. *Mangalorea hopeae*, adult female : spiracle, with warts and 5-locular disc pores (SEM photograph ; the upper side of the picture is the posterior direction of the body).
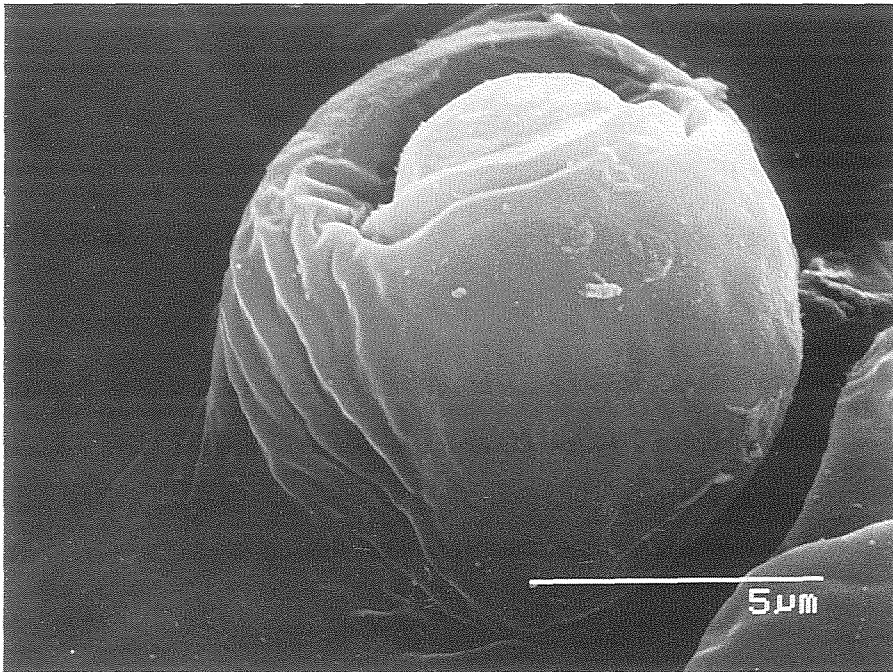
Fig. II.13. *Mangalorea hopeae*, adult female: wart (SEM photograph; part of Fig. II.12).
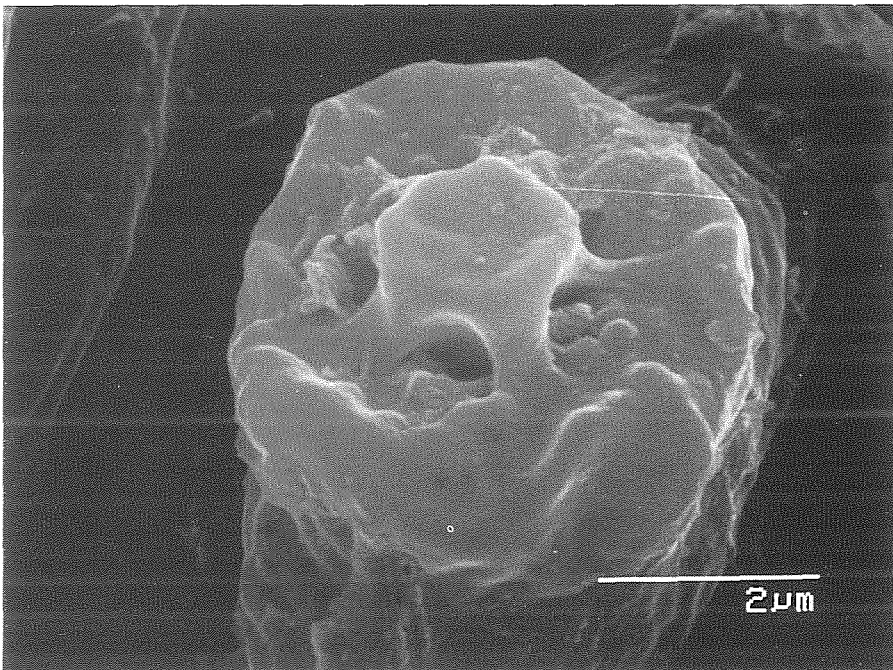

Fig. II.14. *Mangalorea hopeae*, adult female: 5-locular disc pore (SEM photograph; part of Fig. II.12).
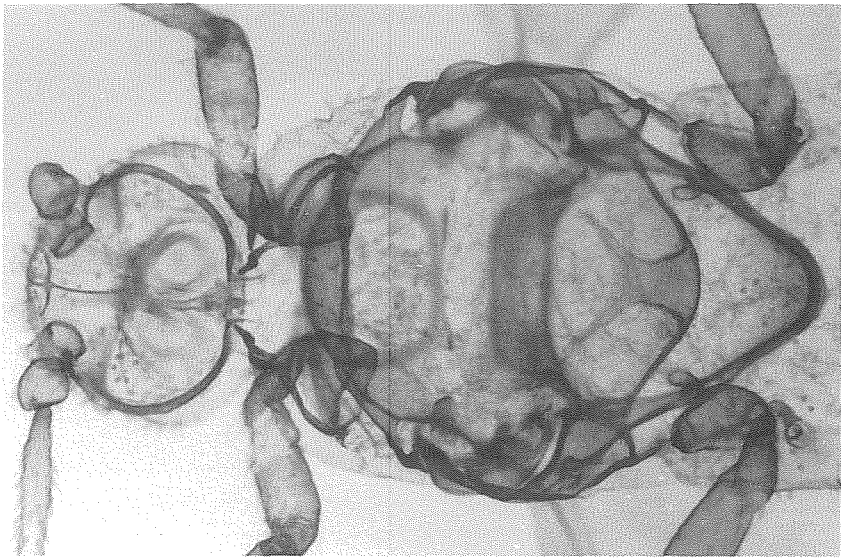
Fig. II.15. *Mangalorea hopeae*, adult male : head and thorax.
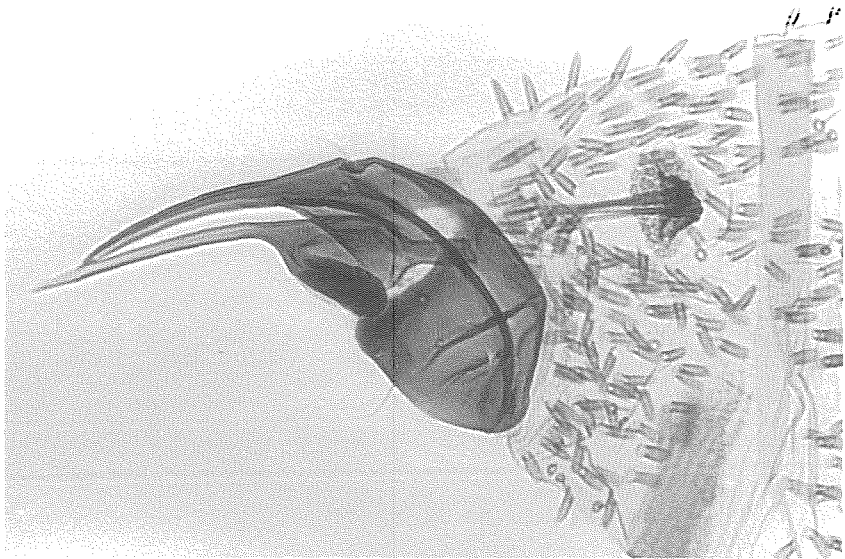

Fig. II.16. *Mangalorea hopeae*, adult male : apex of abdomen.

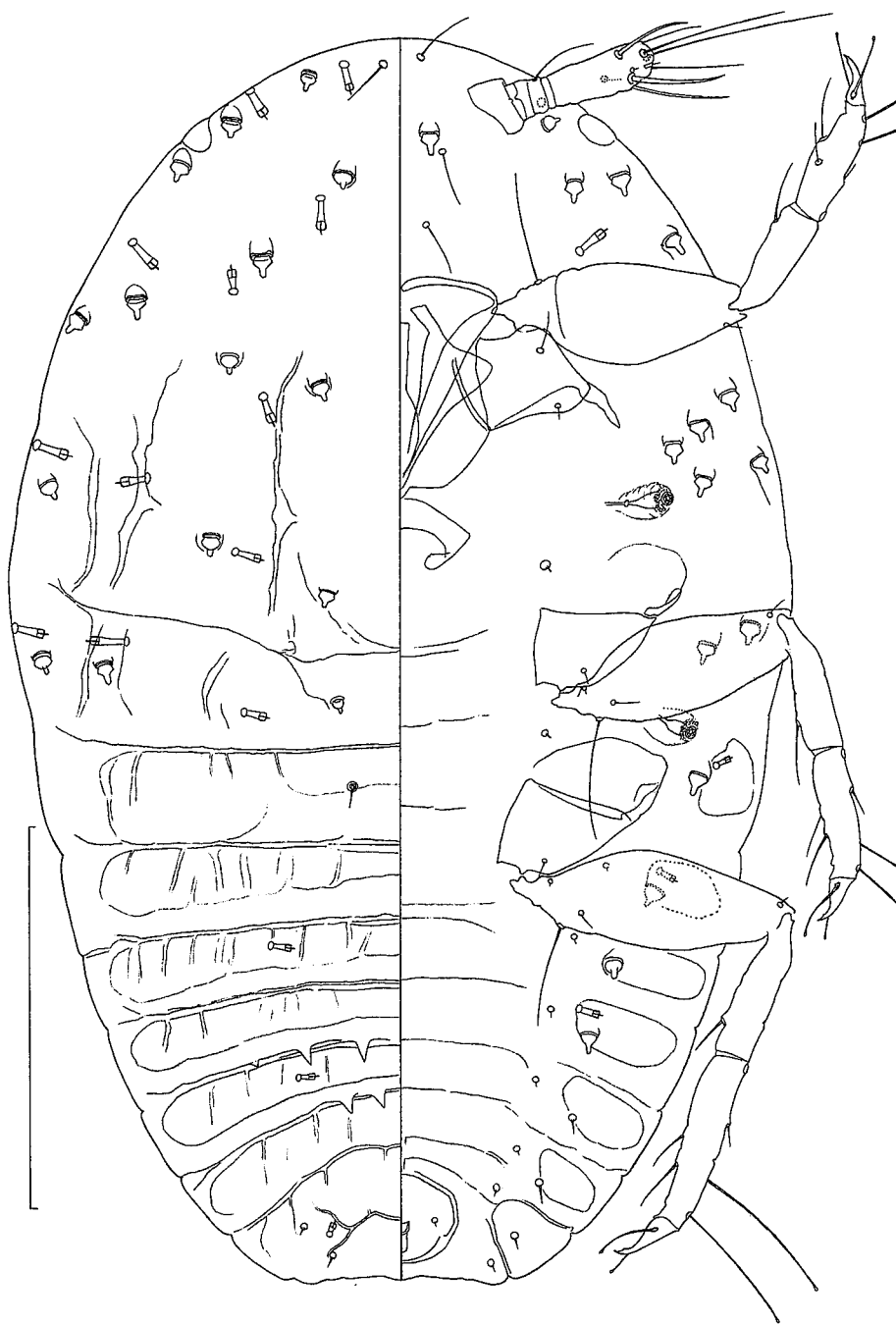Fig. II.17. *Mangalorea hopeae*, 1st instar female (scale : 0.1 mm).

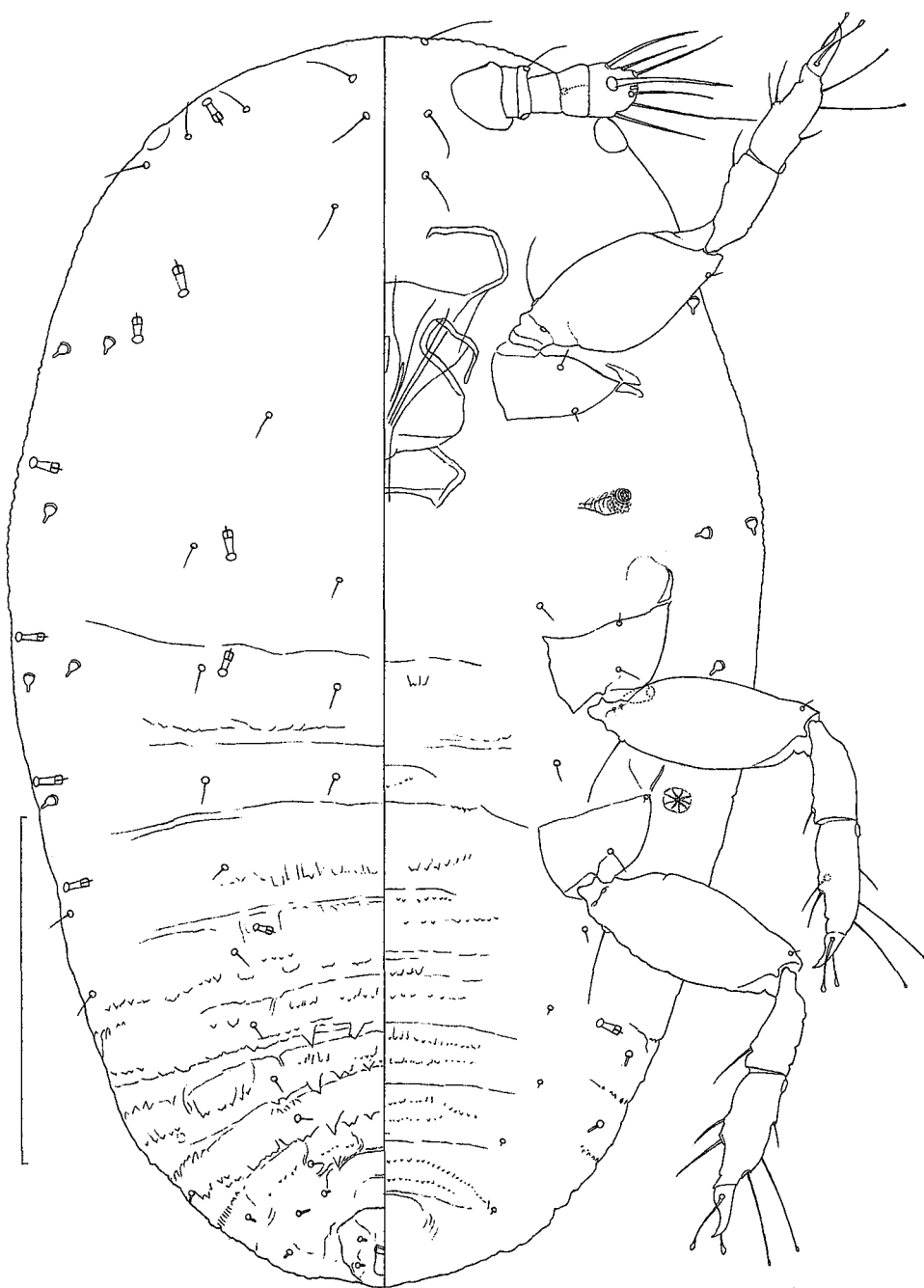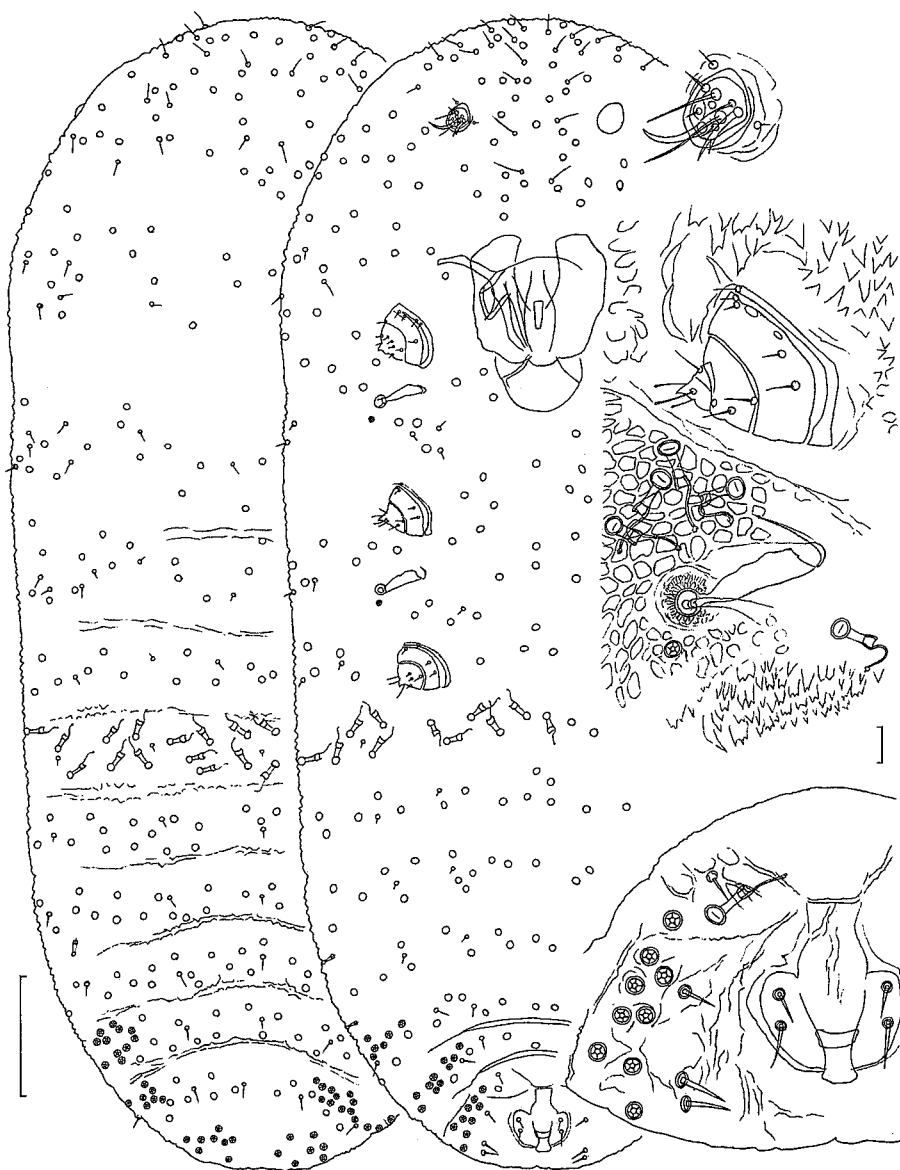Fig. II.18. *Mangalorea hopeae*, 1st instar male (scale : 0.1 mm).

Fig. II.19. *Mangalorea hopeae*, intermediate instar male (scale for body: 0.1 mm; for parts: 0.01 mm).
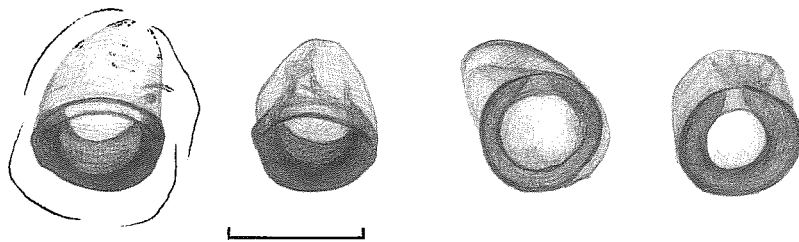
Fig. II.20. *Mangalorea hopeae*, adult female : warts in different views (scale : 0.01 mm).
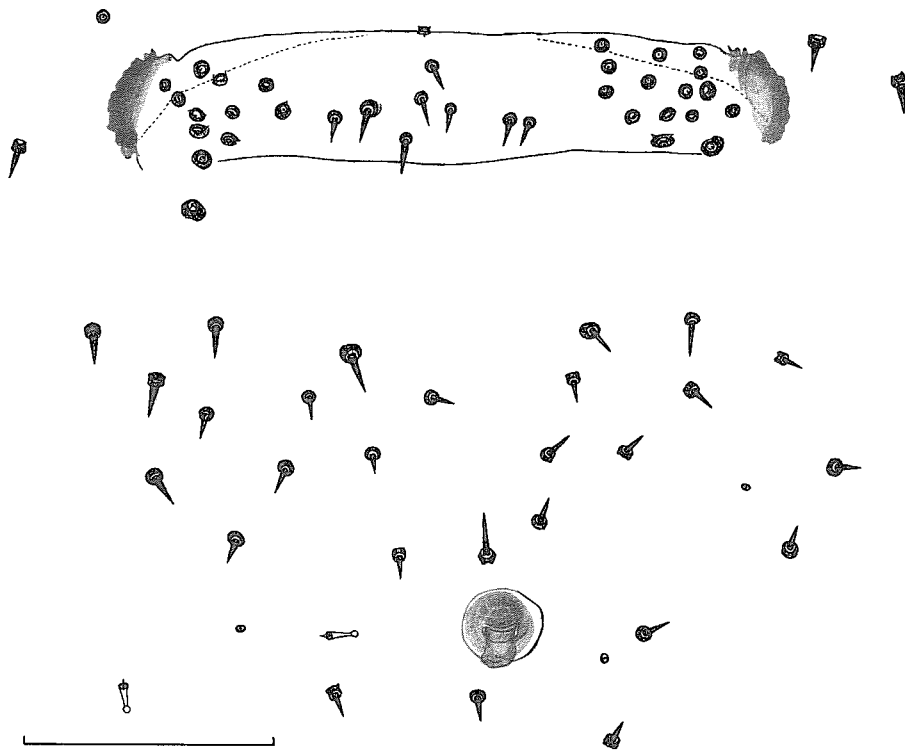

Fig. II.21. *Mangalorea hopeae*, adult female : anal-genital area (scale : 0.1 mm).
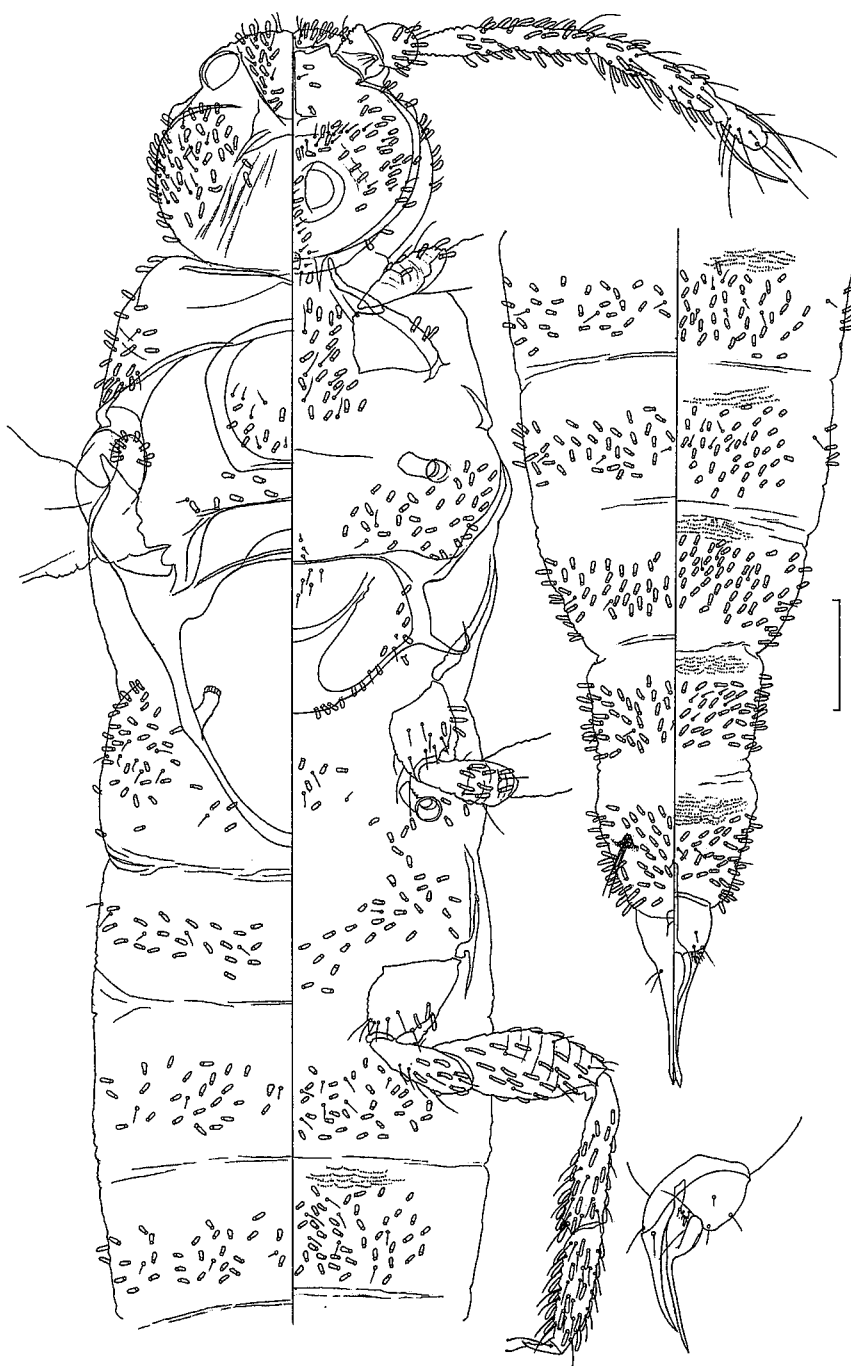
Fig. II.22. *Mangalorea hopeae*, adult male (scale : 0.1 mm).

female' of *B. dipterocarpi* may correspond to them.

One mounted specimen of *M. hopeae* probably belonging to an intermediate instar of the female is available.   It is affected by fungi, and is distorted on the slide.   It is similar to the adult female but simpler in structure : body globular, without legs ; antennae absent (?) ; derm beset with warts ; small ducts of geminate-pore type here and there ; spiracular disc pores 5-locular, 1 or 2 pores associated with each spiracle ; anal plate with a pair of small setae on margin ; anus with operculum on anterior margin ; some acorn-shaped setae around anal plate.   In having both warts and acorn-shaped setae it comes between the 1st instar and the adult female, and there is little doubt that it represents an intermediate instar of the female.   But it resembles none of the intermediate instar females of *Beesonia*.

Intermediate instars of male.   Green (1926) described 'female of third instar' of *B. dipterocarpi,* but later he (Green, 1928) corrected it to the male.   It has 2-jointed antennae and well-developed legs, and, in my view, may belong to the 2nd larval instar.   The intermediate instar male of *M. hopeae* described in this paper is characterized by having tubercular antennae and conical legs, and may belong to another instar — the 3rd instar (the last larval instar).   No further comparison, therefore, is made here.

Adult female.   Green (1926) described 'adult female' of *B. dipterocarpi.*   Later, he (Green, 1928) described 'partly developed adult', but this may in reality be the 3rd instar larva.   In fact, these descriptions do not agree.   If the form described and illustrated in his 1926 paper is really the adult female, *B. dipterocarpi* remarkably differs from *M. hopeae* in the following characters of the adult female : 'notable structures are collected upon and immediately around the small posterior promi-nence' ; the anterior spiracles are much larger than the supposed posterior ; and 'a close tuft of six long and relatively stout setae' arises from within a densely chitinous ring of the anus.   It seems, however, that these species are similar in the structure of the genital area.   In *B. napiformis* and *B. brevipes* the adult female remains within the skin of the 3rd instar, and is entirely membranous and feature-less.   In this respect they are quite different from *B. dipterocarpi* (as based on Green, 1926) and *M. hopeae*.

Adult male.   The adult male of *B. dipterocarpi* described by Green (1926) is apterous, while that of *M. hopeae* is macropterous.   Differences between them, therefore, should be taken with some reservation.   The adult males of these species agree in having 3-segmented antennae, but differ in the details of the 3rd segment.   In *M. hopeae* the halteres are absent in spite of the well-developed wings.   If the halteres are really present in the apterous *B. dipterocarpi* as described by Green, the absence of halteres may be adopted as a generic character of *Mangalorea*.   In *M. hopeae* the tibia and tarsus are articulated, whereas in *B. dipterocarpi* they are fused, but I suspect the fusion to be associated with the apterous (and, therefore, pedes-trian) condition.   Above all, *M. hopeae* is unique in having papillae over the body, but this character alone is insufficient to recognize the genus as distinct.

In conclusion, *M. hopeae* in comparison with the *Beesonia* species is well char-acterized in the 1st instar female and is also unique in some characters of other stages.   This is sufficient to show that *Mangalorea* is distinct from *Beesonia*.   However, comparisons remain incomplete except in the 1st instar female.   Our knowledge of these unusual coccoids is still meagre and fragmentary.   The concepts

of the genera and even the family itself are still to be established.

SUPPLEMENTARY NOTES

1) I (Takagi, 1987) once supposed that the adult female of *B. dipterocarpi* might be a featureless form entirely covered by the skin of the 3rd larval instar as in the oak-associated species, *B. napiformis* and *B. brevipes*. In the present study I identified the adult female of *M. hopeae* on the basis of the presence of embryos and the absence of any trace of another instar (e.g., another set of mouth-parts and spiracles) within its body. It is simplified in structure, but not so much as in the oak-associated species. As already stated, the form described by Green (1926) as the adult female of *B. dipterocarpi* has a structure which may be similar to the genital area of the *Mangalorea* adult female, and now I am inclined to believe that he (Green, 1926, not 1928) was correct in identifying the adult female.

The extremely simplified adult female, which shows no external feature except for the spiracles and mouth-parts, may, therefore, be peculiar to the oak-associated species. Now it is likely that these species do not belong to *Beesonia*. If they represent another genus, the name *Trichococcus* Kanda, 1941 (nec Borchsenius, 1948) [name-bearing species : *Xyloccocus napiformis*] is available.

2) The 'warts' in the adult female, observed by scanning electron microscopy, are unique in structure. They are distributed almost over the body, but no warts exist where setae occur and no setae are found where warts occur. In the supposed intermediate instar female examined (probably belonging to the 3rd instar), warts are replaced by acorn-shaped setae near the anal plate. It seems, therefore, that the warts are modified setae and that the double fold at the base of the 'head' corresponds to the basal socket.

3) The anal operculum, found in the 1st instar male and female, the intermediate instar male and female examined (probably belonging to the last larval instar) and the adult female, is also a unique structure. It is noteworthy that there are no well-developed anal setae in all these instars. In the 3 species of *Beesonia* the anal operculum is absent, whereas the anal setae are prominent in the larval instars.

The wart and anal operculum are not only unique but also undoubtedly derivative. *Mangalorea* is a good taxon, being characterized by these structures among others.

4) Hoy (1963) examined specimens of *B. dipterocarpi* labelled 'co-type' and referred *Beesonia* tentatively to the family Eriococcidae. According to him the 'second-stage nymph' exhibits 'typical eriococcid features particularly tubular ducts'. I am uncertain what his 'second-stage nymph' is. However, the intermediate instar male examined of *M. hopeae* has 2 types of tubular ducts : some ducts are of the geminate-pore type, while others are very similar to the ducts of the families Eriococcidae, Coccidae and Aclerdidae. Some characters of the *M. hopeae* adult male also suggest a relationship to the Eriococcidae. Detailed morphological analysis for clarifying the phylogenetic relationship is, however, beyond the scope of the present paper.

5) The 2nd and 3rd instar females of '*B. quercicola*' (=*B. napiformis*) present 'the most remarkable morphological developments to be found anywhere in the Coccoidea' (Ferris, 1950). Morphological peculiarities in the gall-inhabiting stages

can be understood in connection with the cryptic mode of life. In *M. hopeae* the 1st instar and the adult male, free-living stages, also show unusual characters.

The caudal setae are absent in the 1st instar male and female of *M. hopeae* in spite of their universal presence in the superfamily. In fact, the other known species of the Beesoniidae have well-developed caudal setae. (The caudal setae may be present and reduced to small setae in *M. hopeae,* but I could not identify them.) The adult male of *M. hopeae* is strange in having many papillae on the head, antennae, thorax, legs and the unusually elongate abdomen. This is remarkable, because it is generally admitted that adult male Coccoidea are uniform in the same taxonomic groups and, nevertheless, the *B. dipterocarpi* adult male has no papillae.

The long caudal setae are comparable to the silk threads of spiders in the gossamer flight, apparently contributing to aerial transportation of crawlers. Does their absence indicate another means of dispersal (especially for the female crawlers)? Some coccoids are fantastic in dispersal. Mealybugs of the genus *Hippeococcus* are 'ant-riders' (Reyne, 1954). Gullan and Cockburn (1986) reported the phoretic dispersal of *Cystococcus* 1st instar females by means of clinging to the elongate abdomen of the adult male.*

Then does the elongate and densely papillose body of the adult male of *M. hopeae* mean that the 1st instar female is phoretic on the adult male? In this connection Raman's statement (Part I: Comment 2 and 3) that male larvae feed on their maternal gall is interesting (this behaviour of the male is harmonious with the absence of caudal setae). Here is suggested the male offspring's much earlier appearance, which is prerequisite for enabling them to transport their sisters. The presence of sexually matured but unmated adult females at the emergence time of adult males is another prerequisite. In fact, the galls sent by Raman were various in size, thus probably representing various developmental stages of the female insects within.

6) I collected echinate galls, somewhat similar to those of *M. hopeae*, from *Shorea falcifera* and *S. glauca* [Dipterocarpaceae] at Kuantan, Peninsular Malaysia. I have found, however, that the gall-maker belong to the family Eriococcidae. Beardsley (1971) erected *Gallacoccus* for 2 gall-inhabiting eriococcid species collected from '*Shorea pauciflora*' in Singapore; galls induced by them are like 'small fir cones' and 'drupes', respectively, thus much differing from the galls from Kuantan in external appearance. In Sarawak I collected a few drupelike galls induced on *Hopea sangal* by another eriococcid. According to Raman (pers. commun.), Docters van Leeuwen (1925) recorded a gall with 'many angular scalelike parts' on the surface, thus shaped like a bread-fruit, as occurring on *Dipterocarpus tuberculatus* in Thailand. Raman also 'saw a herbarium sheet of *Shorea oblongifolia* with a gall, more similar to the galls on *Dipterocarpus tuberculatus* reported by Green'; he has made out that 'this has been collected from northwestern Sri Lanka'.

7) The described species of the Beesoniidae are associated with dipterocarps or oaks. Another beesoniid inhabits stem galls on *Shorea curtisii* in Singapore (Anthony, 1974). The eriococcid genus *Gallacoccus,* mentioned above, 'seems most similar to *Reynvaania* Reyne, a genus which contains single named species found in Java in

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* Dr Penny Gullan sent to me the following communication: — 'In this regard, you asked whether the first-instar female of *Cystococcus* has caudal setae. The answer is yes, but these setae are rather weak and short (<100 μm long).'

galls on *Quercus lineata'* (Beardsley, 1971). Other similar gall-inhabiting eriococcids, *Fulbrightia* and *Ollifiella,* occur on *Quercus* in China and southwestern United States, respectively (Ferris, 1950).

Another case of the dipterocarp-oak combination in host association is known in the leaf-mining microlepidopterous genus *Chrysocercops* [Gracillariidae] : of the 14 described species 12 are associated with dipterocarps, while the other 2 species, occurring in Japan and Peninsular Malaysia, respectively, feed on oaks (Kumata, 1992).

The families Dipterocarpaceae and Fagaceae are not closely related phylogenetically. However, according to Ashton (1988), they are similar ecologically ('Dipterocarp ecology remarkably recalls that of Fagaceae'). In East Asia oaks are scattered among dipterocarps in lowland tropical forests, which are replaced by oak-dominant forests at higher altitudes and at higher northern latitudes. It may not be unexpected, therefore, that some insect groups are associated with both dipterocarps and oaks in East Asia. So far as known, however, the Beesoniidae and *Chrysocercops* are restricted to these plant families; then what is the reason for this restriction ?

8) Raman sent me several specimens of another coccoid collected 'on mature branches of *Hopea'*. This coccoid probably belongs to *Pedroniopsis*. I mounted a few other specimens of this coccoid from galls of *M. hopeae.* The material is too scanty to know whether this association is accidental or not. *Pedroniopsis* was erected by Green (1926) for *P. beesoni,* which he described from Madras as occurring on *Shorea robusta,* and has been supposed to belong to the Eriococcidae.

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